



## A differential prey response to invasive lionfish, *Pterois volitans*: Prey naiveté and risk-sensitive courtship



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### ABSTRACT

The assimilation of behavioral and evolutionary processes into conservation management provides insights into how invasive predators affect native fauna. The Indo-Pacific lionfish (*Pterois volitans*) has caused extensive reduction in the abundance of small-bodied reef fish within their introduced range. One possible mechanism facilitating this high predation rate may be due to prey exhibiting evolutionary naiveté toward this invasive predator. Here, we tested for the potential role of prey naiveté by examining the behavioral response of a prey species, the beaugregory damselfish (*Stegastes leucostictus*), toward this invasive predator. Damselfish demonstrated invasive predator recognition and subsequent anti-predator behavior, which may attenuate the impact posed by this invasive predator. However, damselfish under predation threat failed to modulate courtship behavior in the presence of lionfish. Therefore, benefits derived from the ability to recognize and respond appropriately to lionfish may be of little consequence if damselfish are unable to curtail high-risk courtship behavior in their presence.

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### 1. Introduction

Non-indigenous species are capable of disrupting habitat (Vivrette and Muller, 1977), hybridizing with or displacing native species (Echelle and Connor, 1989; Rhymer and Simberloff, 1996), altering community structure and reducing biodiversity (Mack et al., 2000; Vitousek et al., 1996). Negative impacts of non-indigenous species can be even more pronounced with invasive predators, which can be a major catalyst in the decline or extirpation of native prey populations (Grosholz et al., 2000; Kats and Ferrer, 2003; Knapp, 2005; Knapp and Matthews, 2001; Wiles et al., 2003). For example, the predatory Nile perch (*Lates niloticus*) introduced into Lake Victoria during the 1950s contributed to the extinction of roughly 200 haplochromine cichlid species (Witte et al., 1992). Relative to terrestrial and freshwater systems, studies investigating the ecological impacts of non-indigenous species in marine and estuarine environments are underrepresented (Grosholz et al., 2000). With reported increases in the frequency and distribution of non-indigenous species, concerns are being raised about potential impacts on local marine ecosystems (Cohen and

Carlton, 1998; Molnar et al., 2008; Rilov and Crooks, 2009; Ruiz et al., 2000).

The invasive Indo-Pacific lionfishes (*Pterois volitans* and *Pterois miles*), first observed off the southern coast of Florida during the 1980s (Morris and Akins, 2009), are the first invasive marine fish to become established in the North Atlantic Ocean and the Caribbean Ocean (Morris and Akins, 2009; Schofield, 2009). The distribution of *P. miles* appears to be localized off the United States east coast while *P. volitans* (hereafter referred to as lionfish) has been rapidly expanding throughout the Caribbean Ocean (Freshwater et al., 2009). Because lionfish are carnivorous generalists exhibiting rapid population growth in their invaded range, these predators are posing major concerns for local coral reef ecology (for review see: Côté et al., 2013). For example, Albins and Hixon (2008) demonstrated that the presence of lionfish in the Bahamas reduced recruitment to coral fish communities by 80%. Additionally, Green et al. (2012) reported that an increase in lionfish abundance was correlated with a 65% reduction in the local biomass of small-bodied reef fish in the Bahamas.

What enables non-indigenous species to be such effective predators? One factor contributing to the success of invasive predators may be due to prey naiveté, although lack of local predators, competitors, or parasites in their invaded range may also play a role (Cox and Lima, 2006; Mack et al., 2000; Mitchell and Power, 2003; Salo et al., 2007; Torchin et al., 2003). For lionfish, prey naiveté has been suggested as a likely element contributing to the documented predation success within their invaded range (Albins, 2013; Albins and Lyons, 2012;

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Cure et al., 2012; Jud and Layman, 2012; Jud et al., 2011). Because of their cryptic coloration/movement, elongated pectoral fins to “corral” prey and the use of focused jets of water to temporarily confuse prey (Albins and Hixon, 2013; Albins and Lyons, 2012), their unique predator archetype may be a major factor in the exhibition of prey naiveté (Cox and Lima, 2006).

Evolutionary prey naiveté has been suggested to transpire from the absence of exposure to a novel predator over evolutionary time (Cox and Lima, 2006), resulting in nonexistent or ineffective anti-predator behavior in their presence (Gamradt and Kats, 2002; Smith et al., 2008) and ultimately contributing to their high predation rate (Salo et al., 2007; Sih et al., 2010). For example, Gomez-Mestre and Díaz-Paniagua (2011) demonstrated that Iberian green frogs (*Pelophylax perezi*) failed to exhibit anti-predator behavior in response to an invasive predator (*Procambarus clarkii*) and as a result suffered increased mortality compared to a native predator (*Anax imperator*).

In fishes, predator recognition leads to anti-predator behavior such as an increase in refuge use, predator avoidance, shoaling behavior as well as changes in movement that reduce the probability of predation (Alvarez and Nicieza, 2003; Botham et al., 2006; Ferrari et al., 2005; Helfman, 1989; Mitchell et al., 2011). Because predation eliminates any chance of future fitness, selection favors behavioral plasticity in the presence of predators (Torres-Dowdall et al., 2012) even at the cost of immediate reproductive success (Lima and Dill, 1990).

Animals often experience increased predation risk during reproduction due to augmented breeding colors, conspicuous displays, or reduction in vigilance (Lima and Dill, 1990; Magnhagen, 1991). Risk-sensitive courtship has been well documented in teleosts, which typically entails a reduction, or cessation, of reproductive behaviors in the presence of native predators (e.g., Candolin, 1997; Chivers et al., 1995; Figueira and Lyman, 2007; Magurran and Seghers, 1990). Modification of reproductive activities has also been demonstrated by “acoustical avoidance” behavior, which likewise entails a reduction, or cessation, of mating calls in the presence of predators (Luczkovich et al., 2000; Remage-Healey et al., 2006).

However, risk-sensitive courtship is dependent on the ability to detect and recognize a known predator. Because of this, naïve prey may not only lack appropriate anti-predator behavior but may also fail to reduce courtship in the presence of a recently invaded predator. To address this, we examined the anti-predator behavior and risk-sensitive courtship in the beaugregory damselfish (*Stegastes leucostictus*) under different social conditions. We chose this subject model for two reasons: 1) damselfish are frequently preyed upon by lionfish (Layman and Allgeier, 2012; Morris and Akins, 2009), making them an excellent test species to examine prey naiveté and 2) to our knowledge, it is unknown if beaugregory damselfish exhibit risk-sensitive courtship behavior.

We first quantitated the behavioral response of damselfish to a native predator and non-predator to define an appropriate anti-predator response. Using these response variables, damselfish were then exposed to predators (native/invasive) of varying sizes to see if they demonstrated graded anti-predator behavior in their presence. For the exhibition of risk-sensitive courtship, we examined if male acoustic and courtship behavior varied under predation threat of a native or invasive predator. Opposed to native predators, we predicted that damselfish would fail to view lionfish as a threat and exhibit neither anti-predator behavior nor risk-sensitive courtship in their presence.

## 2. Materials and methods

### 2.1. Study site and subject model

The study was conducted July 2011 in the west back reef of Discovery Bay, Jamaica (18.4667° N, 77.4000° W) where the first verified sighting of lionfish occurred in 2008 (Dayne Buddo; pers com). Male beaugregory damselfish permanently defend small territories (1–2 m) and aggressively defend these sites against other male damselfish, egg predators,

as well as herbivores (Itzkowitz, 1990; Leese et al., 2009; Santangelo et al., 2002). Males attract nearby females through a conspicuous courtship display that entails a characteristic “dip” swimming movement in combination with a change in dorsal pigmentation (Haley et al., 2004) and acoustic signaling (Albrecht, 1981, 1984; Spanier, 1979). Beaugregory damselfish produce multi-pulsed, broadband signals commonly called “chirps” during antagonistic interactions (Myrberg and Spires, 1972) as well as in courtship displays (Albrecht, 1981, 1984; Spanier, 1979). If a male is successful in enticing a female to enter his territory, she then inspects his nest site and lays adhesive eggs in a crevice. Males are then left to tend and guard the developing eggs until they mature into planktonic larva 5–7 days later.

The ecology of Discovery Bay consists of a shallow heterogeneous sand and rubble habitat. The natural breeding sites used by beaugregory damselfish are highly variable, generally consisting of a small piece of rubble with a smooth crevice used for egg deposition. Since breeding site quality has been documented to affect levels of aggression as well as courtship (Itzkowitz and Haley, 1999; Leese et al., 2009; Snekser et al., 2009), habitat quality was standardized by using artificial nest sites. These artificial sites were manufactured by using four 15 cm lengths of 10 cm diameter white PVC tubing arranged perpendicularly and then bolted onto a 30 cm square plastic sheet. Males have been shown to favor these artificial sites over natural breeding sites, and will quickly inhabit and actively defend these structures (Santangelo et al., 2002).

At the onset of the study, 15 artificial sites were placed on the substrate adjacent to actively defended natural territories. When males moved into these artificial sites, they were then given a numbered tag. Male beaugregory damselfish are rarely usurped from their territory (Itzkowitz et al., 1995), so by tagging an artificial site we were able to effectively analyze the same male’s behavior following exposure to different stimuli. Behavioral observations were recorded in response to predator stimuli over the course of 3 weeks.

### 2.2. Experimental protocol

The Lehigh University Institutional Animal Care and Use Committee approved all experimental protocols (No. 148). Using cast and long handled nets, stimuli were haphazardly collected outside of the study site each day and released after experimental use with the exception of lionfish, which were sacrificed at the conclusion of the study. Territorial males were presented with a single stimulus each morning followed by a different stimulus in the afternoon, which has been shown to be a sufficient time interval to prevent focal male habituation (Itzkowitz, 1990). The observed order of tagged males (i.e., 1-15/15-1) was alternated each day and the presentation order of size class, stimuli species, and females were randomized throughout the study. Each trial began after an observer(s) placed the stimulus on the substrate, level with the artificial site, and moved 2 m away. Damselfish behavior does not appear to be influenced by the presence of an observer at this distance (Itzkowitz, pers obs). A 3-min trial period was chosen because it facilitates adequate response time to the stimulus yet is temporally short enough to permit testing multiple sequential territorial males and has been utilized in other studies (e.g., Little et al., 2013; Santangelo and Bass, 2010; Snekser et al., 2009).

### 2.3. Characterization of anti-predator behavior

To first define how beaugregory damselfish behaved in the presence of a predator, a live sand diver (*Synodus intermedium* [mean Total Length 261.8 mm ± 35.4 Standard Error, n = 3 replicates]) was presented to each territorial male [TL 79.7 mm ± 0.8]. The sand diver is a sit and wait predator that commonly preys upon damselfish (Mitchell et al., 2011; Ferrari et al., 2011; M. Itzkowitz, pers obs). To outline an appropriate anti-predator response in damselfish, responses to the herbivorous parrotfish (*Scarus taeniopterus* [TL 119.5 mm ± 38.5, n = 2]), a common territorial intruder, were used as a comparison. A non-

predator was used to account for the presence of a larger fish within the focal male's territory, which has been utilized to characterize anti-predator behavior in other studies (e.g., Bass and Gerlai, 2008; Marsh-Hunkin et al., 2013). Due to the large size and long lateral shape, parrotfish and sand diver stimuli were each placed in a 46 cm long clear plastic tube that was 10 cm in diameter and closed at each end with a monofilament net.

Following capture, each stimulus species (i.e., parrotfish or sand diver) was presented to each tagged male by positioning it at substrate level 0.3 m away from each artificial site for 3-min timed observations. During each timed observation, we recorded two mutually exclusive behaviors: time spent in refuge and intruder proximity. "Time spent in refuge" was defined as the total time the focal male spent within, or directly above, the 30 cm perimeter of the artificial site and "intruder proximity" was defined as the amount of time the focal male spent within one body length of the stimulus. Since we were ultimately limited in the number of variables we could record underwater, we chose these two response variables because we felt they unambiguously represented the response tendencies of focal males. However, it is important to point out that males could be engaged in alternative behaviors during each trial.

#### 2.4. Prey naiveté

To assess how anti-predator responses may differ in the presence of a native vs. an invasive predator, a lionfish or a sand diver was presented individually to males in their artificial sites. For each predator, two size classes were assigned (small and large) to represent varying degrees of threat. These size classes were used to examine the exhibition of a graded, or threat sensitive response (Chivers et al., 2001; Helfman, 1989). Four different stimulus groups were used: 1) small sand diver [TL 140 mm  $\pm$  40, n = 2] 2) large sand diver [TL 283 mm  $\pm$  22, n = 2] 3) small lionfish [TL 85 mm  $\pm$  10, n = 2] and 4) large lionfish [TL 187 mm  $\pm$  7, n = 3]. While each predator stimuli was selected based upon an approximate 50% body length difference between size classes (i.e., small or large), size distinctions between predator species were difficult to control for due to difference in morphological shape and stimuli availability.

Following capture, lionfish were placed in 2-liter clear bottles with holes drilled into the lid (to facilitate both water transfer as well as release of olfactory cues) and sand divers were placed in the same containers as in the previous experiment. Each predator was placed individually 0.3 m away from a given artificial site and for each 3-min observation "time spent in refuge" and "intruder proximity" was recorded. Throughout our experiment, predators appeared to behave normally in their respective container; lionfish were able to fan out their pectoral fins and the sand divers were able to maintain a typical "sit and wait" orientation. While the use of different containers was unavoidable due to differences between stimuli body shape, differences in stimuli movement/container type may have affected focal male behavior. A major time constraint in the field stemmed from difficulty in locating, and/or capturing, predator species (especially of ideal size). In order to allow sufficient time for stimulus capture prior to each session (i.e., morning/afternoon), we reduced the number of observed territorial males (n = 7) for each stimulus presentation.

#### 2.5. Risk-sensitive courtship

To evaluate the exhibition of risk-sensitive courtship, we repeated the methods from the previous experiment but in combination with a female beaugregory damselfish [TL 66.0 mm  $\pm$  2.1, n = 4]. During each timed observation, we recorded two key behaviors: "time spent in refuge" and "intruder proximity". To further examine male reproductive behavior, a "female only" condition was added to establish a baseline of male reproductive behavior. Presentations were as follows: 1) a female with a sand diver (small and large), 2) a female with a lionfish

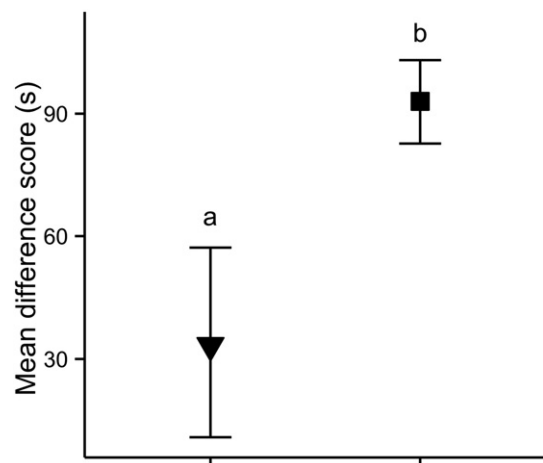
(small and large) and 3) a female only. An empty bottle was not used as a control with the female alone condition as male beaugregory damselfish infrequently approach empty bottles or display aggressive behavior toward them (Haley and Müller, 2002; Itzkowitz, 1990; Little et al., 2013).

Again, each trial was timed for 3-min and the following behavioral data were recorded: "time spent in refuge", "intruder proximity", female proximity and number of dips. "Female proximity" was defined as the time spent within one body length of the female and the number of "dips" was recorded as discrete events each time the focal male swam forward and down followed by a rapid upward jump in the water column. This transpires in conjuncture with a change in dorsal pigmentation, and only occurs during courtship.

Recordings of vocalizations occurred during behavioral presentations of the female alone or when paired with a large predator (native or invasive). The total number of calls produced and the total time spent calling within a 2-min period were recorded to investigate if/how males modulate vocalization behavior under predation threat. The hydrophone was placed within 20 cm of the artificial site and sounds were recorded with a hydrophone (Aquarian H2a-0) coupled to a SONY digital audio recorder (linear PCMM10) with a sampling rate of 44.1 kHz. To control for acoustic disturbances, vocalization datum were taken 15 s after the start of the recording and any noise disruptions were skipped over for a total of 2-min of data for each 3-min recording. Acoustic data was analyzed using Raven Pro 1.4 bioacoustics software (The Cornell Lab of Ornithology, Ithaca, NY).

#### 2.6. Statistical analysis

One of the tagged males was displaced by another species of damselfish half way through the experiment and was excluded from the analysis. For each behavioral variable, all replicates were averaged together and statistically analyzed by mean focal male response. Individual outcome variables for "number of dips", "female proximity" and each acoustic measure were analyzed in SPSS using ANOVAs and/or two tailed t-tests. Experiments that recorded two outcome variables ("time in refuge" and "intruder proximity") used a "mean difference score", which was calculated by subtracting "intruder proximity" from "time in refuge" and analyzed in SPSS using an ANOVA and/or two tailed t-tests. To account for potential type 1 errors due to pairwise t-tests,  $\alpha$  was set at 0.025. All graphics were constructed using "R".

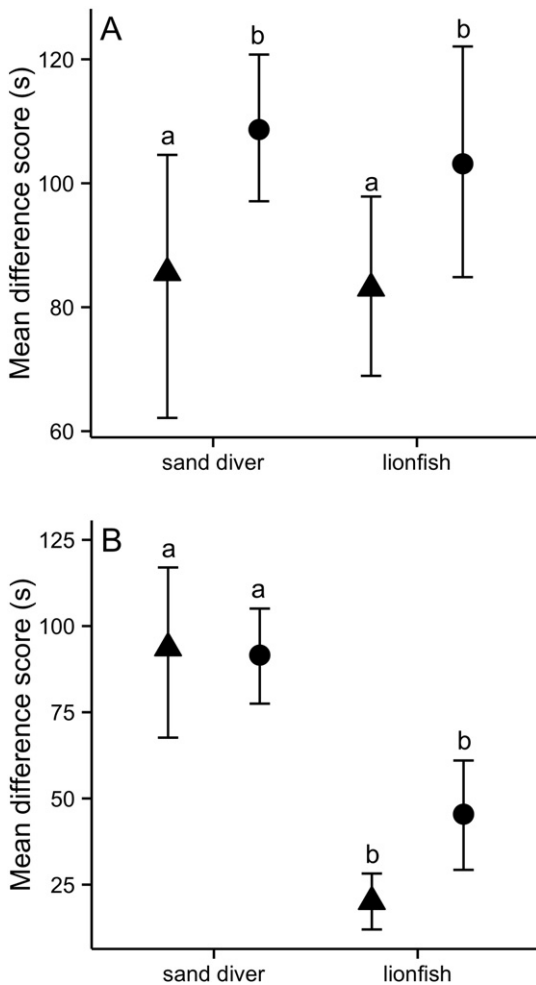


**Fig. 1.** Characterization of anti-predator behavior. Focal male behavior in the presence of a non-predator (parrotfish ▼) or a native predator (sand diver ■). Mean difference score was calculated by subtracting "intruder proximity" from "time in refuge". Error bars represent the 95% confidence interval. Letters indicate statistical significance ( $p < 0.025$ ).

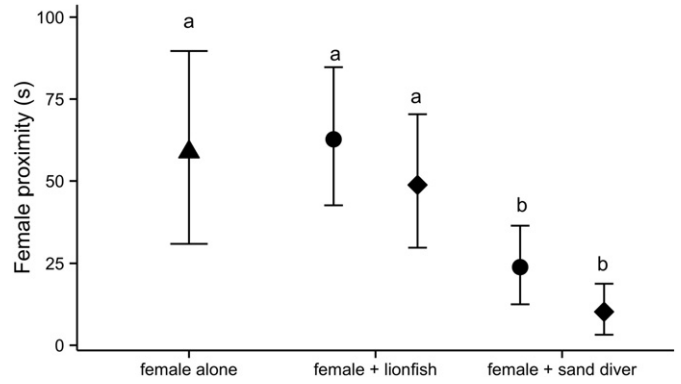
### 3. Results

Overall, positive mean difference scores indicated that on average territorial males spent more time in the refuge than in close proximity to intruders. A significant paired t-test ( $t_{13} = 4.46$ ,  $p = 0.001$ ) indicated that this tendency was greater with the native predator opposed to the non-predator (Fig. 1). Male difference scores showed a significant main effect for size (ANOVA;  $F_{1,6} = 19.48$ ,  $p = 0.005$ ), which were similar in magnitude when exposed to either native or invasive predators as indicated by the non-significant predator species  $\times$  size interaction ( $F_{1,6} = 0.03$ ,  $p = 0.864$ ) (Fig. 2a). With the addition of a female, the main effect of intruder species was significant (ANOVA;  $F_{1,6} = 105.54$ ,  $p < 0.001$ ) with a greater mean difference score in the presence of the sand diver compared to the lionfish (Fig. 2b). No main effect of size (ANOVA;  $F_{1,6} = 1.46$ ,  $p = 0.273$ ) or predator species  $\times$  size interaction ( $F_{1,6} = 1.41$ ,  $p = 0.280$ ) was shown in the presence of a female and predator (Fig. 2b).

Pairwise t-tests showed that males spent similar time in close proximity to the female alone as they did compared to the female + lionfish ( $t_6 = 1.16$ ,  $p = 0.289$ ) and the female + small lionfish ( $t_6 = 0.33$ ,  $p = 0.754$ ). However, when compared to the female alone condition, time was significantly reduced in the presence of the female + large



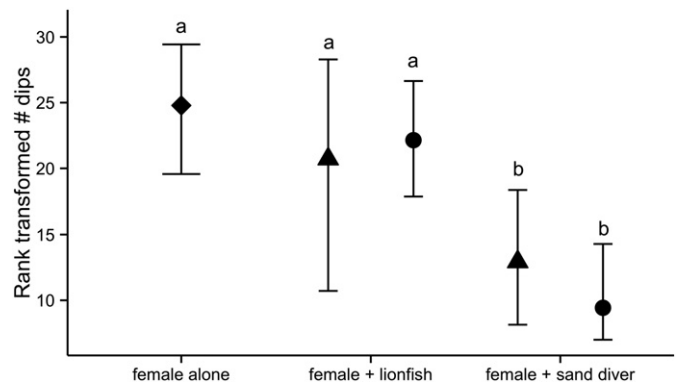
**Fig. 2.** Prey naivete. a) Focal male behavior in the presence of small ▲ or large ● native (sand diver) or invasive (lionfish) predators and b) focal male behavior when predators were simultaneously paired with a female damselfish. Mean difference scores were calculated by subtracting “intruder proximity” from “time in refuge”. Error bars represent the 95% confidence interval. Letters indicate statistical significance ( $p < 0.025$ ).



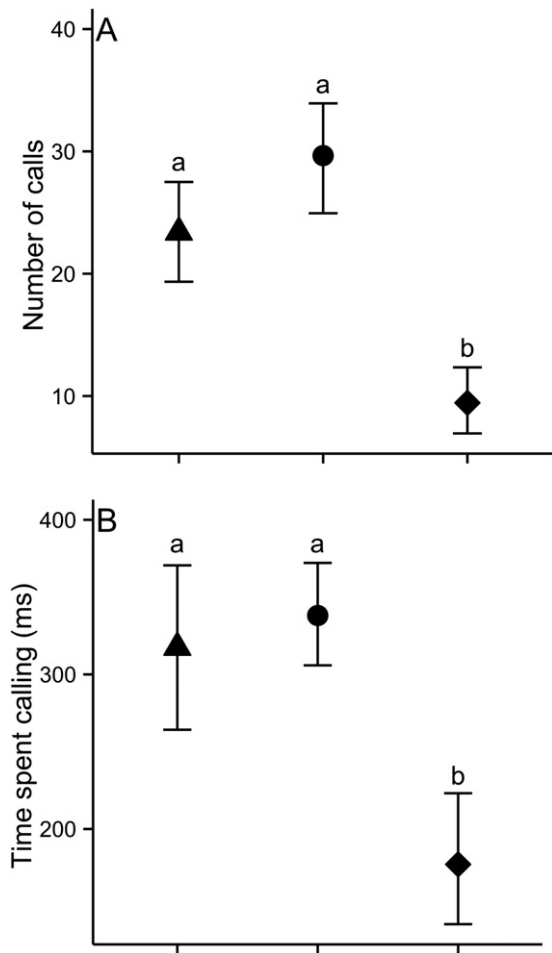
**Fig. 3.** Risk-sensitive courtship. The time focal males spent within one body length of a female alone ▲, or a small ● and large ◆ invasive (lionfish) or native (sand diver) predator. Error bars represent the 95% confidence interval. Letters indicate statistical significance ( $p < 0.025$ ).

sand diver ( $t_6 = 3.61$ ,  $p = 0.011$ ) but not the female + small sand diver ( $t_6 = 2.87$ ,  $p = 0.028$ ) (Fig. 3). The number of courtship dips was too low to permit application of parametric tests so a Friedman 2-way ANOVA was used to analyze the data. Results indicated a significant difference in the number of dips in the 5 groups ( $\chi^2_4 = 16.46$ ,  $p = 0.002$ , Fig. 4). Compared to the number of dips in the female alone condition, the presence of a sand diver significantly depressed the number of dips with the female + large sand diver ( $Z = 2.37$ ,  $p = 0.018$ ) but not the female + small sand diver ( $Z = 2.20$ ,  $p = 0.028$ ) (Wilcoxon Signed Ranks Tests).

A repeated measures ANOVA showed that the female alone, female + lionfish, and female + sand diver groups differed in mean number of calls ( $F_{2,16} = 15.35$ ,  $p < 0.001$ ). Pairwise t-tests showed that there was no difference between the female alone compared to the female + lionfish ( $t_8 = 0.59$ ,  $p = 0.569$ ) but the female + sand diver condition showed a significant decrease in the number of calls when compared to the female alone and the female + lionfish conditions ( $t_8 = 3.71$ ,  $p = 0.006$  and  $t_8 = 8.50$ ,  $p < 0.001$ , Fig. 5a), respectively. The 3 groups also differed in mean time spent calling ( $F_{2,16} = 19.58$ ,  $p < 0.001$ ). Again, there was no difference between the female alone vs. the female + lionfish condition ( $t_8 = 1.46$ ,  $p = 0.184$ ), but each differed from the “female + sand diver” for the “female alone” ( $t_8 = 5.08$ ,  $p = 0.001$ ) and the “female + lionfish” ( $t_8 = 7.79$ ,  $p < 0.001$ ; Fig. 5b).



**Fig. 4.** Risk-sensitive courtship. The number of dips territorial males performed to a female in the presence or absence of a small ▲ or large ● invasive (lionfish) or native (sand diver) predator. Rank transformed for normality. Error bars represent the 95% confidence interval. Letters indicate statistical significance ( $p < 0.025$ ).



**Fig. 5.** Acoustic avoidance behavior. Vocalization of territorial males in the presence of a female alone ▲, a female + lionfish ● or a female + sand diver ◆ a) number of calls and b) time spent calling. Error bars represent the 95% confidence interval. Letters indicate statistical significance ( $p < 0.025$ ).

## 4. Discussion

### 4.1. Prey naiveté

In order for prey to show an adaptive response to a predator, the ability of prey to first recognize a predator as a threat is necessary (Ferrari et al., 2008; Sih et al., 2010). Based upon a comparable mean difference score to both native and invasive predators, our results demonstrated that damselfish are able to recognize invasive lionfish as a potential threat. Furthermore, damselfish exhibited approach/avoidance behavior based upon the size of both native and invasive predators, supporting an accurate assessment of the degree of threat posed by both predator species (Dugatkin and Godin, 1992; Helfman, 1989).

The ability of prey to recognize an invasive predator and assess the degree of threat strongly opposed our initial predictions. However, in an environment as heterogeneous and diverse as the coral reef, the plasticity of prey to recognize and respond appropriately in the presence of a predator can be critical for their survival. This plasticity is demonstrated by Mitchell et al. (2011), who reported that a species of damselfish (*Pomacentrus moluccensis*) rapidly learned to recognize multiple novel predator cues following recruitment to the reef. Since damselfish in Discovery Bay have only been in contact with lionfish since 2008, well within a single generation for damselfish, associative learning may be enabling prey to rapidly identify lionfish as a potential predator. With numerous examples of plastic morphological and behavioral responses to invasive predators (reviewed in Strauss et al., 2006), this raises the

interesting prospect that local marine communities may possess the ability to rapidly adapt to the threat of a novel or invasive predator. This is critical since elimination of established invasive marine species is typically impractical (Thresher and Kuris, 2004).

Other studies investigating prey responses to lionfish have reported variable results. Marsh-Hunkin et al. (2013) reported that two gobies (*Coryphopterus glaucofraenum* & *Coryphopterus thompsoni*) increased refuge use in the visual presence of lionfish compared to a native predator (Nassau grouper) or a non-predator (French grunt) in a series of laboratory experiments. These results demonstrated that gobies exhibited the ability to visually recognize lionfish as a potential threat. However, Lönnstedt and McCormick (2013) demonstrated that juvenile damselfish collected in the native range of lionfish failed to respond to either their chemical and/or visual cues and as a result exhibited reduced survivorship in a series of laboratory experiments. We suggest that perhaps variation in the reported presence/absence of anti-predator behavior in response to lionfish may be due to differences in: Temporal/spatial exposure in their natural habitat, Ontogeny (i.e., juvenile/adult), experimental response variable, or environment (i.e., laboratory/field experiments). At this point, we can only speculate on the variable results documented to date.

If indigenous prey species do in fact lack the ability to recognize invasive lionfish as a threat, this should have been revealed by elevated predation rates and/or changes in hunting activity in their invaded vs. native range. However, a study by Cure et al. (2012) reported comparable lionfish predation rates, activity levels as well as time budgets (e.g., time hunting) in their native vs. invaded range. Relatedly, Hackerott et al. (2013) failed to find an association between lionfish abundance and biotic resistance (competitive exclusion or predation by resident predators) throughout the Caribbean, suggesting that a lack of predators also may not be a primary factor contributing to the invasion success of lionfish. Interpreting the results of the preceding studies with our results indicates that perhaps neither predator release or prey naiveté are major factors contributing to the documented success these predators are having in their invaded range.

### 4.2. Risk-sensitive courtship

Predator induced effects on prey can exert consumptive effects (direct predation) and non-consumptive effects (indirect effects such as prey dispersal, reduced feeding rates and vigilance; for reviews see: Creel and Christianson, 2008; Lima, 1998). While the consumptive effects of introduced predators have been extensively studied, non-consumptive effects are receiving increased attention (for review see: Sih et al., 2010). Curtailed reproductive behavior can be classified as a non-consumptive effect and can exact an obvious toll on prey fitness. Our results clearly demonstrated that the presence of a native predator (i.e., sand diver) exerted a non-consumptive effect on prey reproductive behavior. This was demonstrated by a decrease in courtship behavior (dips), time spent in close proximity to the female as well as time spent vocalizing in the presence of a large native predator. While this risk-sensitive behavior can reduce predation susceptibility, it also can exact a toll by reducing the reproductive success of male damselfish.

Interestingly, invasive predator recognition did not extend to the context of risk-sensitive reproductive behavior, suggesting that this is a less plastic response. Despite the apparent invasive predator recognition damselfish demonstrated in the presence of lionfish, they chose to disregard this potential threat in favor of reproductive success. Along the same vein, Marsh-Hunkin et al. (2013) showed that two species of gobies failed to reduce feeding rates when exposed to the chemical/visual cues of lionfish. While failure to alter feeding rates or courtship behavior prevents a non-consumptive effect, this is of note because it offers a potential avenue for increased predation susceptibility during these behaviors. In damselfish, susceptibility could be especially pronounced since lionfish predation rates and activity levels occur primarily during crepuscular periods (Green et al., 2011) and are highest in the

morning (Morris and Akins, 2009), which coincides with peak courtship times in damselfish (Petersen and Hess, 1991).

While the acquisition of learned predator recognition can occur rapidly (e.g., Chivers and Smith, 1995), it seems that further experience may be required for recently introduced predators to evoke risk-sensitivity in reproductive behaviors. To our knowledge, this is the first report of deficiencies in risk-sensitive courtship in response to an invasive predator. Since damselfish demonstrated invasive predator recognition, yet failed to extend it to a reproductive context, this suggests that there may be differential rates of learned predator recognition. Perhaps responding to the presence of a novel predator while engaged in reproductive behavior utilizes a different neurological process or requires an evolutionary history with a given predator. Irrespective of the potential causation, examination of risk-sensitive courtship can add an additional layer in the support/rejection of the ability of prey to respond appropriately in the presence of a novel predator. Moreover, because of the potential impacts that this behavioral deficiency may exert on prey survivorship, susceptibility during reproductive behavior can also be investigated as a potential pathway for invasive predator success.

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## Glossary

- Acoustical avoidance*: A reduction of acoustic calls in the presence of predators.
- Evolutionary prey naïveté*: Prey naïveté stemming from the absence of exposure to a novel predator over evolutionary time. This can result in the inability to recognize a predator as a threat or exhibit nonexistent or ineffective anti-predator behavior in their presence.
- Dip*: A conspicuous courtship display that male damselfish use to attract females. It entails a characteristic jump in the water column in combination with a change in dorsal pigmentation.
- Predator archetype*: Similar phenotypic traits (behavioral or morphological) belonging to a set of predator species and anti-predator responses that are adaptive in their presence. Generally, similarities in predator archetype have been demonstrated in predators belonging to the same family.
- Predator recognition*: Sensory cues used to accurately assess the presence (and threat level) of a predator.
- Risk-sensitive courtship*: A reduction, or cessation, of reproductive behaviors in the presence of predators.